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Nest Architecture, Immature Stages, and Ethnoentomology of a New Species of *Trigonisca* from Northern Colombia (Hymenoptera: Apidae)

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ABSTRACT

Stingless bees (Apinae: Corbiculata: Meliponini) are biologically and culturally important pollinators within the tropical and subtropical areas of the world. However, limited information is available for the majority of the species. Biological and systematic data are presented for a new species of *Trigonisca* Moure, from the arid region of La Guajira, Colombia. The genus is part of the distinctive *Trigonisca* genus group, noteworthy for its position as the earliest diverging extant lineage of neotropical stingless bees. We briefly diagnose the genus group and provide a key to the genera and subgenera of the *Trigonisca* genus group, along with the description of *Exochotrigona* Engel, new subgenus. We also outline the species occurring in Colombia and present a description for *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, including accounts of all three castes. A single, poorly preserved egg is noteworthy because of its extremely small size. Its chorion

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is extensively covered by a surface pattern of elevated geometric figures, as seems to be characteristic of the Meliponini. The robust mature larva, though remarkably small, exhibits extensive spiculation of dorsal body surfaces and most body segments with small, paired dorsolateral tubercles. In addition, the labral apex exhibits an apical patch of recently discovered multipronged spicules intermixed with various sensory sensilla. These morphological features of immature stages, where known, are similar to those previously reported for other Meliponini. We document the internal architecture of nests of *T. mepecheu*, which we found in trunks of *Stenocereus griseus* (Haw.) Buxb. (Cactaceae) and more commonly in *Libidibia coriaria* (Jacq.) Schltdl. (Fabaceae), along with nests of the only other stingless bee from La Guajira, *Melipona favosa* (Fabricius). Nests were also found in the sides of manufactured structures. The indigenous Wayúu harvest stingless-bee honey and have specific names in Wayuunaiki for the two species occurring in the region, although there is apparently an oral tradition in which the honey of *T. mepecheu* causes blindness. *Trigonisca* (*Trigonisca*) *ameliae* Penney from Colombian copal is a new junior synonym of *T.* (*T.*) *schulthessi* (Friese).

INTRODUCTION

Stingless bees (Meliponini) are biologically and culturally important pollinators within the tropical and subtropical areas of the world (Nogueira-Neto, 1953; Heard, 1999; Michener, 2007; Ramírez et al., 2018). However, limited information is available for the majority of the species and this is particularly true for the more minute taxa, such as those of the genera *Hypotrigona* Cockerell and *Liotrigona* Moure of the Afrotropics, the tropical Asian *Lisotrigona* Moure and *Pariotrigona* Moure, and *Trigonisca* Moure in the New World tropics. These are, of course, not the only minute stingless bees, but these genera include species that are exclusively on the smaller end of the size spectrum and typically share a suite of traits associated with such reduction (e.g., reduced wing venation, brood cells arranged in clusters), although achieved independently rather than through a shared history (Michener, 2001). Despite their diminutive proportions such species remain important pollinators, and, where known, encompass unique natural histories that enrich our understanding of the range of bee biology (e.g., Bassindale, 1955; Bänziger, 2018; Bänziger and Bänziger, 2010; Bänziger et al., 2009, 2011). Moreover, stingless bees are often cultivated by indigenous peoples in those countries where they occur, sometimes with considerable integration into local culture, mythology, and religion (e.g., Posey, 1983a, 1983b, 1983c; Posey and Camargo, 1985; Ayala et al., 2013; Gonzalez et al., 2018).

Here we describe a new species of *Trigonisca* from the La Guajira Peninsula of northern Colombia and provide an account of its immature stages and nesting biology. The La Guajira Peninsula, which juts out into the Caribbean Sea, borders northwestern Venezuela and includes Punta Gallinas, the northernmost extension of mainland South America. The region is distinctive for its generally xeric climate with expanses of desert and scrub habitat. It is also home to the Wayúu, the largest indigenous tribe of people in Colombia and whose territory has historically encompassed the peninsula along with some bordering areas in both Colombia and Ven-

FIGURE 1. Map of La Guajira Department and neighboring areas in northern Colombia, with inset showing location of map within Colombia (rectangle). Pink outline defines the territory of the Wayuú, the dots the location where nests of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, were found, with the green dot representing the type locality. Map produced using the SimpleMappr tool (Shorthouse, 2010).

ezuela (fig. 1). The Wayúu have a distinctive language, Wayuunaiki (Maipuran language family), and like most indigenous groups a rich culture and body of traditions associated with life in the xeric landscape. Not surprisingly, the local Wayúu were familiar with the stingless bees of their region and we provide what little ethnoentomological information we were able to ascertain during our field studies.

Trigonisca is part of the distinctive *Trigonisca* genus group, which also includes the extinct genus *Exebotrigona* Engel and Michener from the Eocene (Moure, 1950; Engel and Michener, 2013). The *Trigonisca* genus group is noteworthy for its position as the earliest diverging extant lineage of neotropical stingless bees (Rasmussen and Cameron, 2010). Moure (1950) proposed four genera (*Celetrigona* Moure, *Dolichotrigona* Moure, *Leurotrigona* Moure, and *Trigonisca*) for the more than 45 species that later Michener (2007) synonymized under the genus *Trigonisca*. Camargo and Pedro (2005, 2009), Albuquerque and Camargo (2007), and Pedro and Camargo (2009) revised the majority of the species in these four groups, although those in *Trigonisca* s.str., the most species rich of the four, remain to be explored. Despite morphological differences among groups, Michener (2007) did not recognize them at the subgeneric nor generic level, as he did for many other neotropical meliponines.

While morphological and molecular studies support the monophyly of the *Trigonisca* genus group, the monophyly of some of its species groups is not. For example, the analysis of Rasmussen and Cameron (2010) indicated the likelihood that *Leurotrigona* s.l. is paraphyletic. Herein, we recognize some of the species groups at the subgeneric level and propose a new subgenus. We briefly diagnose the genus group and provide a key to the subgenera of the *Trigonisca* genus group, along with the description of the new subgenus. We briefly outline the species occurring in Colombia and present the description of a new species (fig. 2), including accounts of all three castes.

MATERIAL AND METHODS

Field studies were conducted during November 2016 by M.S.E., V.H.G., and P.A.S.-C. of wild bees in La Guajira Department, Colombia (fig. 1), a region encompassing largely desert and scrub habitat. During this survey, two species of stingless bees were found, one of which was an undescribed member of the *Trigonisca* genus group. For the descriptions of the adult stages the morphological terminology is adapted from Engel (2001), Michener (2007), and Rasmussen et al. (2017). Measurements were taken using an ocular micrometer on an Olympus SZX-12 stereomicroscope and are reported for the holotype worker, with ranges of variation from paratypes provided in parentheses except a single measurement is presented for the unique queen paratype and only a range is provided for drone paratypes. Photographs were taken with a Canon EOS 7 digital camera with various microscopic lens attachments, and illuminated by a Xenon flash. When reporting specimens and label data, we have used standard translingual symbols for sexes and castes (e.g., Engel and Rasmussen, 2017; Rasmussen et al., 2017), and specifically ♀ for the sterile worker caste. Specimens of the new species have been distributed amongst the following institutional repositories (curators listed in parentheses):

AMNH Division of Invertebrate Zoology, American Museum of Natural History, New York (J.G. Rozen, Jr.)
BBSL Bee Biology and Systematics Laboratory, USDA-ARS, Utah State University, Logan (T.L. Griswold)
CSCA California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento (K. Williams)
FSCA Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Gainesville (E. Talamas)
ICNC Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santa Fé de Bogotá (F. Fernández)
IIRB Instituto de Investigación de Recursos Biológicos, Alexander von Humboldt, Villa de Leyva, Colombia (C. Gomez-Posada)
LABUN Laboratorio de Investigaciones en Abejas, Departamento de Biología, Universidad Nacional de Colombia, Santa Fé de Bogotá (R. Ospina)
LIPI Museum Zoologicum Bogoriense, Indonesian Institute of Sciences, Bogor, Indonesia (S. Kahono, D. Peggie)
PCYU Packer Collection, York University, Toronto, Canada (L. Packer)
SEMC Division of Entomology (Snow Entomological Collection), University of Kansas Natural History Museum, Lawrence (M.S. Engel)
ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin (M. Ohl)

Larvae and a single, poorly preserved egg were studied with light and scanning electron microscopy, the latter using a Hitachi S5700 in the microscopy and imaging facility of the American Museum of Natural History.

To document the internal nest structure for this species, we dissected one of the nests that was inside a living tree of *Libidibia coriaria* (Jacq.) Schltdl. (Fabaceae), locally known as a divi-divi tree. We closed the nest entrance and removed the portion of the branch that contained the nest, placing the nest in a plastic bag and freezing it at a local butcher shop for 24 hr until dissection. We used pocketknives, axes, and chisels, and measured internal features with a caliper. To estimate the total number of brood cells, we divided the weight of the total group of cells by that of a single cell. We examined brood cell contents using a stereomicroscope and counted all adults. Mean values are given with ranges and standard deviations. Angelo Gomez Sijona, a native Wayúu, who is bilingual in Spanish and Wayuunaiki, helped us transcribe the common names.

SYSTEMATICS

Trigonisca Genus Group

The *Trigonisca* genus group clade, comprising the extant genus *Trigonisca* and the extinct genus *Exebotrigona*, is united by the combination of a minute body size, with a length typically 4.5 mm or frequently less, and a forewing length of 4 mm or less; a distinctly broadened base to the marginal cell, with a basal angle (angle formed within the marginal cell between pterostigmal margin and r-rs) of 68°–90°, and the marginal cell, at tangent of pterostigmal apex, broader than submarginal cell area; the posterior margin of the metatibia nodulose or tuberculate, sometimes weakly so (apparently not nodulose in *Exebotrigona*), owing to prominent bristle bases; and the setae of the inner surface of the metabasitarsus arranged in transverse rows (Michener, 1990, 2007).

Presently, there are 45 species contained in the *Trigonisca* genus group, including the species described herein, and these are arranged into four subgenera, which are sometimes treated as distinct genera (e.g., Moure, 1950). The analysis of Rasmussen and Cameron (2010) indicated the likelihood that *Leurotrigona* s.l. is paraphyletic, and so is treated as two distinct groups herein. *Leurotrigona* s.str. and *Exochotrigona*, new subgenus, each with two species (Pedro and Camargo, 2009; see below), while *Celetrigona* has four species (Camargo and Pedro, 2009) and *Trigonisca* s.str. (= *Dolichotrigona* Moure) has 37 (Albuquerque, 1990; Ayala, 1999; Albuquerque and Camargo, 2007; Camargo and Pedro, 2005; Alvarez and Lucia, 2018; herein). Five species of the group are currently recorded as occurring within Colombia: *Trigonisca* (*Exochotrigona*) *crispula* Pedro and Camargo, *T.* (*Celetrigona*) *longicornis* (Friese), *T.* (*Trigonisca*) *schulthessi* (Friese), *T.* (*T.*) *buyssoni* (Friese), and *T.* (*T.*) *graeffei* (Friese) (Nates-Parra, 2001; Smith-Pardo, 2003; Camargo and Pedro, 2009; Pedro and Camargo, 2009). Examination of numerous workers of *Trigonisca* in Colombian copal (Engel, personal obs.), individuals of which are not uncommonly encountered as inclusions, reveal that they are universally *T. schulthessi*, of which the injudiciously described *T. ameliae* Penney (Penney et al., 2013) is a junior synonym (new synonymy).

Key to Subgenera of *Trigonisca* s.l.

(worker caste)

1. Integument of mesoscutum and mesoscutellum smooth and shiny; preoccipital carina absent; transscutal sulcus between axillae shallowly impressed; mesoscutellum comparatively flat and low, acutely rounded apically in profile and slightly raised above level of metanotum 2
—Integument of mesoscutum and mesoscutellum matt, microalveolate to tessellate; preoccipital carina present at least laterally, sometimes weakly so; transscutal sulcus between axillae deeply and broadly impressed; mesoscutellum gently convex, broadly rounded apically in profile and distinctly raised above level of metanotum 3
2. Malar space as long as 2× flagellar diameter; posterior margin of metatibia gently arched, without projection at distal angle; parapenicillum curved but not greatly sinuate; head width 1.0 mm or greater ..... *Leurotrigona* Moure
—Malar space as long as flagellar diameter; posterior margin of metatibia somewhat sinuous, with distal angle projected; parapenicillum markedly sinuate; head width less than 1.0 mm ..... *Exochotrigona* Engel, n. subgen.
3. Labrum simple; bristles along posterior margin of metatibia as long as or shorter than maximum metatibial width ..... *Trigonisca* Moure, s.str.
—Labrum bituberculate; bristles along posterior margin of metatibia distinctly longer than maximum metatibial width ..... *Celetrigona* Moure

Genus *Trigonisca* Moure

Exochotrigona Engel, new subgenus

TYPE SPECIES: *Leurotrigona pusilla* Moure and Camargo in Moure et al., 1988.

DIAGNOSIS: As for the genus as well as: Small bees, 2.30 mm or less in total body length, forewing length 1.90 mm or less; integument smooth, shining, largely black to dark brown throughout without true yellow maculation, with labrum, clypeus, mandible, scape, tegula, and mesoscutellum sometimes with yellowish to ferruginous areas.

Worker. Head slightly wider than long; clypeus with simple setae; vertex rounded; preoccipital area rounded; scape shorter than torulocellar distance; labrum simple; mandible bidentate; malar space short, as long as flagellar diameter. Transscutal sulcus between axillae shallowly impressed; mesoscutellum comparatively flat and low, acutely rounded apically in profile and slightly raised above level of metanotum; metatibia subtriangular, 2.5–2.6× as long as wide; posterior margin of metatibia somewhat sinuous, with distal angle projected; corbicular setae simple; inner surface with keirotrichiate zone faintly elevated, posterior glabrate zone not depressed; parapenicillum markedly sinuate; metabasitarsus subrectangular, without basal sericeous area on inner surface, with setae arranged in 6–7 transverse rows; forewing shorter than body; hind wing with 5 distal hamuli.

Drone. Metasomal sternum V with apical margin comparatively straight or concave (with deep, broad medial emargination in *Leurotrigona*); sternum VII relatively transverse (subtriangular, trapezoidal, or subrectangular in *Trigonisca* and *Celetrigona*).

ETYMOLOGY: The new subgeneric name is a combination of the Greek *exochos* (meaning, "jutting out"), a reference to the projecting and prominent apical posterior angle of the metatibia, and the generic name *Trigona* Jurine. The gender of the name is feminine.

INCLUDED SPECIES: *Trigonisca pusilla* (Brazil, French Guiana, Peru) and *T. crispula* (Colombia). Both species are diagnosed and described in detail by Pedro and Camargo (2009).

Subgenus *Trigonisca* Moure

Trigonisca* (*Trigonisca*) *mepecheu Engel and Gonzalez, new species

Figures 2–9

DIAGNOSIS: The new species can be distinguished in the worker caste from its congeners by the following combination of traits: mandible bidentate; setae of face and mesoscutum unmodified (fig. 3B) (lacking the modified pomponlike or plumose decumbent setae of species such as *T. nataliae* (Moure) or *T. pediculana* (Fabricius)); setae of scape shorter than diameter of scape (fig. 3B); sculpturing of mesoscutellum distinctly weaker than that of mesoscutum giving the former a shinier appearance (figs. 2A, 3A, C) (versus most other species in which the two are identically sculptured); presence of broad yellowish-orange areas of coloration on clypeus, lower face, paraocular areas, gena, and postgena (figs. 2A, 3B) (integument entirely sooty black in *T. graeffei*: Friese, 1900; Moure, 1950; Albuquerque, 1990); marginal cell not pronouncedly bulky, with r-rs forming slightly acute angle with pterostigma (fig. 4A) (e.g., similar to species such as *T. mixteca* Ayala, *T. intermedia* Moure, and others), i.e., r-rs not completely orthogonal to pterostigma (versus r-rs distinctly orthogonal to pterostigma and forming with 3Rs more pronouncedly bulky U-shaped base to marginal cell, such as in *T. graeffei*, *T. meridionalis* Albuquerque and Camarago, *T. nataliae*, and others: Albuquerque, 1990); R along wing margin beyond pterostigma equal to width of marginal cell at tangent of pterostigmal apex (fig. 4A).

DESCRIPTION: **Worker.** Total body length 2.73 mm (2.33–3.00 mm), forewing length (apex of costal sclerite to wing tip) 2.03 mm (2.00–2.07 mm). Head wider than long, width 1.00 mm (0.98–1.04 mm), length 0.92 mm (0.88–0.93 mm); compound eye length 0.64 mm (0.62–0.65 mm); upper interorbital distance 0.65 mm (0.65–0.69 mm), lower interorbital distance 0.60 mm (0.58–0.63 mm). Scape length 0.40 mm (0.38–0.40 mm), shorter than torulocellar distance, torulocellar distance 0.46 mm (0.46–0.50 mm). Clypeus broader than long, approximately 3.3–3.5× as wide as long, length 0.20 mm (0.20–0.21 mm), width 0.71 mm (0.69–0.71 mm). Malar area prominent, length approximately 1.6–1.8× flagellar diameter. Mandible bidentate, two small, acutely pointed preapical teeth. Metatibia 2.7–2.8× as long as wide, length 0.75 mm (0.75–0.83 mm), maximum width 0.28 mm (0.28–0.30 mm); outer surface gently concave in apical third, forming corbicula. Forewing with marginal cell base broad, basal angle 80°; R

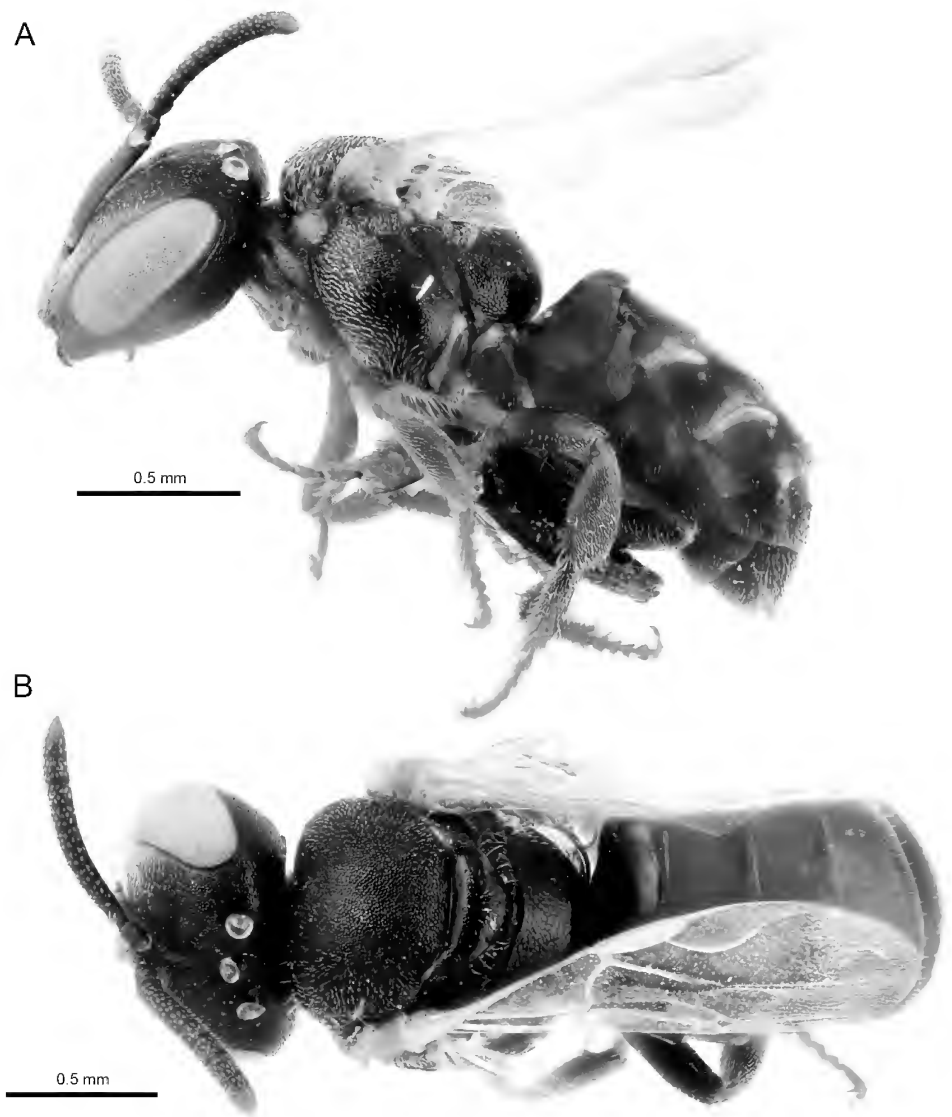


FIGURE 2. Worker of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Lateral habitus. **B.** Dorsal habitus.

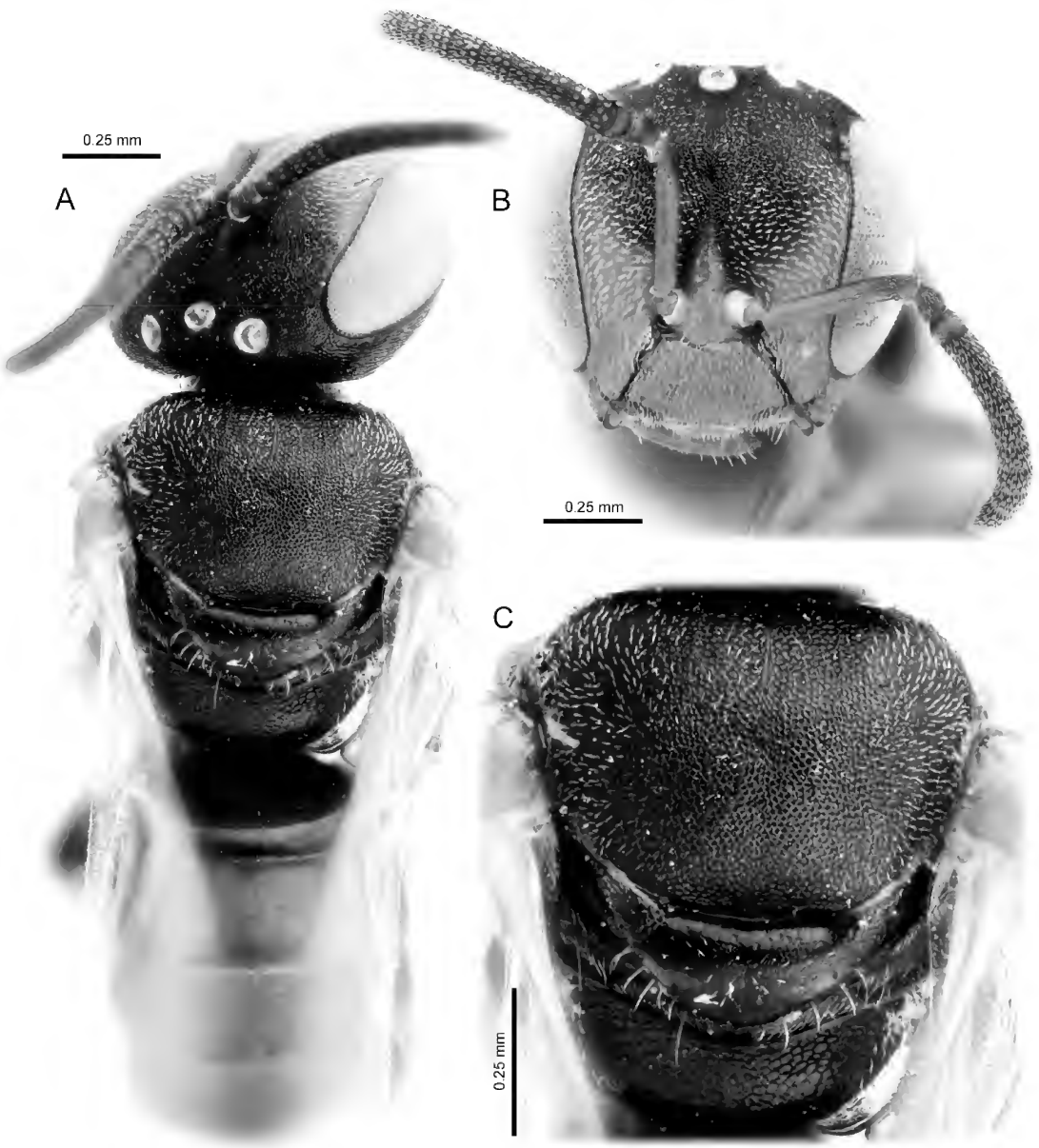


FIGURE 3. Worker of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Dorsal detail of head and mesosoma. **B.** Facial view. **C.** Integumental sculpture of mesosomal dorsum.

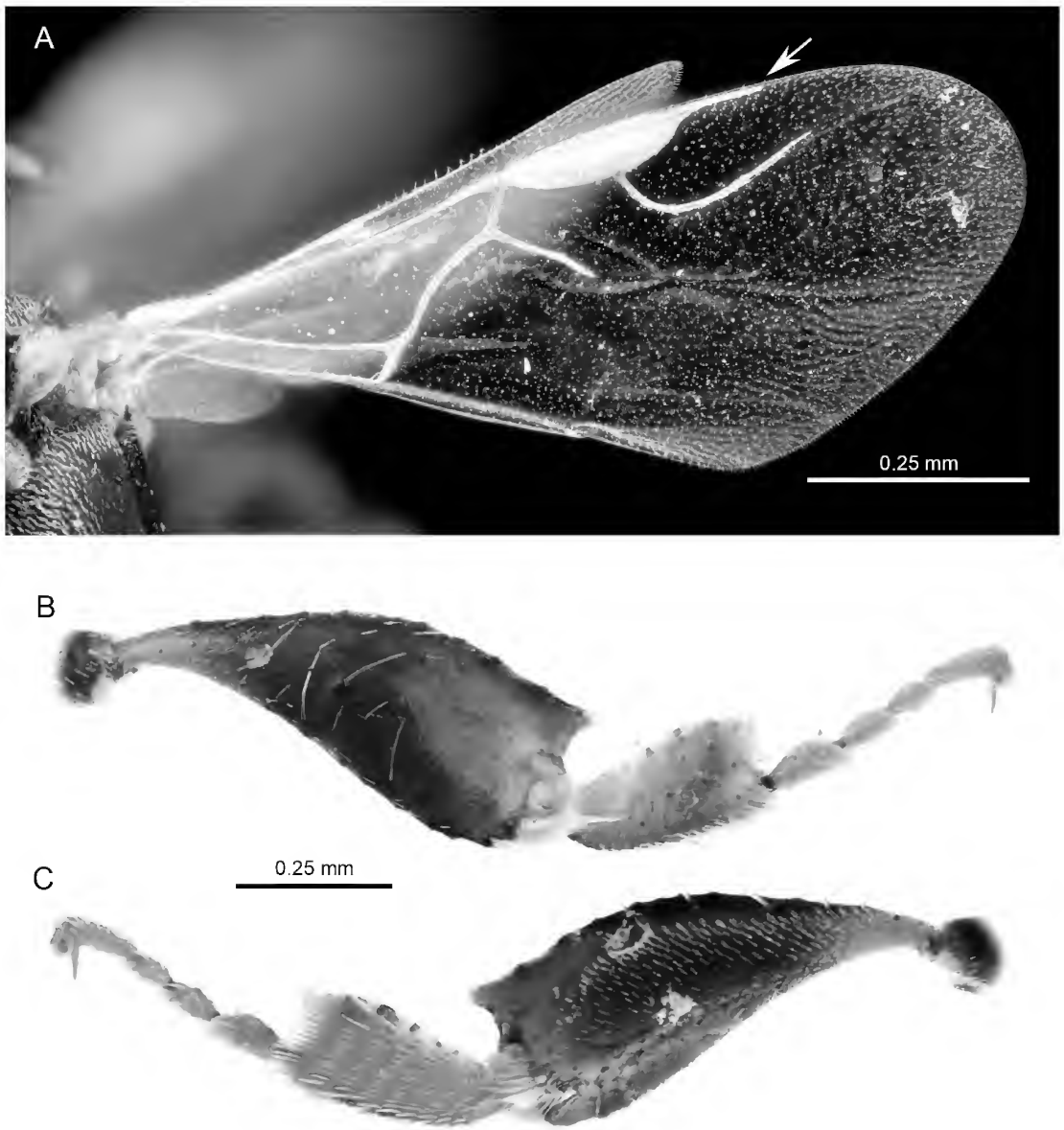


FIGURE 4. Worker of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Forewing (arrow indicates termination of radius on leading edge of wing). **B.** Outer surface of metatibia and metatarsus. **C.** Inner surface of metatibia and metatarsus.

on wing margin beyond pterostigma as long as marginal cell width at pterostigmal apex; hind wing with 5 distal hamuli.

Integument of clypeus and lower face faintly and weakly microalveolate (fig. 3B), such sculpturing becoming more prominent on frons; vertex microalveolate as on frons, blending to weakly coriarious (sensu Harris, 1979) on gena, with such patterning becoming faint ventrally near postgena; postgena smooth. Pronotum faintly microalveolate; mesoscutum distinctly

microalveolate (figs. 2B, 3A, C), with medial line present as weak impression about one-quarter mesoscutal midlength, parapsidal lines short, faintly impressed, about one-third length of medial line; tegula weakly and faintly imbricate; mesoscutellum with deep transverse depression bordering transscutal sulcus with mesoscutum and between axillae, surface faintly microalveolate to smooth; axilla weakly microalveolate, distinctly less sculptured than mesoscutum and appearing shinier; metanotum weakly microalveolate (as on axilla); mesepisternum and metepisternum tessellate (we consider tessellate to be on a gradation with microalveolate whereby the interspaces are larger and less impressed); propodeum tessellate (fig. 3A, C). Metasomal terga impunctate and smooth to weakly and exceedingly faintly coriarious, faintly evident coriarious areas more prominent on terga V and VI and on lateral, ventrally folded portions of terga; sterna weakly and faintly coriarious.

Integument generally black to dark brown (fig. 2A, B) except with yellowish orange on labiomaxillary complex, mandibles, labrum, clypeus, supraclypeal area, malar space, postgena, and lower gena, lower face (below tangent of antennal toruli), and in lower frons and paraocular areas, but not reaching to vertex of compound eye (fig. 3B); antennal scape yellowish orange on lower surface and brown on much of upper surface, particularly apically; pedicel and flagellum brown except light brown to yellowish orange on lower surface of first flagellomere and apex of apical flagellomere. Pronotum yellowish orange with areas of dark brown to black bordering mesoscutum and propleurae (fig. 2A); propleuron yellowish orange with dark brown along midline; mesoscutum black to dark brown; tegula translucent yellow; wing veins pale yellow to off-white, membranes hyaline clear, with iridescent reflections (fig. 4A); mesoscutellum as on mesoscutum except with narrow areas of lighter brown apicolaterally near margin with axillae; metanotum brown to dark brown; mesepisternum and metepisternum dark brown to black; propodeum dark brown to black; foreleg largely yellowish orange with areas of light brown to brown on upper or outer surfaces of profemur and protibia; midleg largely brown except mesotarsus yellowish orange, apical half of mesobasitarsus yellowish orange, and with areas of yellowish orange apically on mesocoxa, on mesotrochanter, basally and apically on mesofemur, and basally on mesotibia; hind leg largely brown to dark brown, except yellowish orange to light brown basally on metatibia, lighter brown on outer surface of metabasitarsus, and yellowish orange on metatarsus. Metasoma largely brown to dark brown, terga I–IV often lighter, either light brown or brown, than dark brown terga V and VI; terga II–IV variably with pale patch at lateral fold; sterna brown to dark brown.

Pubescence generally silvery white. Face with scattered minute, decumbent, silvery-white setae (fig. 3B), such setae largely simple except those of paraocular face below upper frons with some minute branches; vertex posterior to ocelli with a few more prominent, erect, longer, simple setae; setae of scape minute, simple, much shorter than diameter of scape, largely decumbent except a few suberect; gena and postgena sparsely setose, latter virtually bare. Mesoscutum with scattered, decumbent to suberect minute silvery setae (fig. 3C), similar to those of face, some with minute branches; intermixed along anterior borders with longer, erect simple, silvery-white setae, such longer erect setae more sparsely intermingled on mesoscutal disc; mesoscutellum with minute, decumbent setae sparse on disc, with more prominent, elongate, erect, simple, silvery-white

setae posteriorly; metanotum with abundant, decumbent, silvery-white setae not obscuring surface; mesepisternum with minute to short decumbent setae similar to those of mesoscutum, such setae becoming sparser posteriorly and longer ventrally; metepisternum virtually bare, similar to posterior area of mesepisternum; propodeum largely bare except around propodeal spiracle. Setae of legs largely silvery white except more yellowish or yellowish orange on inner surfaces of tibiae and tarsi; elongate silvery, almost translucent, bristles of metatibial posterior margin simple, a few such setae on corbicular surface (fig. 4B); penicillus composed of long, pale yellow setae; rastellum composed of numerous, long, fine, soft setae; parapenicillus composed of elongate, pale yellow setae arching forward, some nearly meeting apex of penicillus. Metasoma sparsely setose; terga I–IV largely bare except for sparse, minute, decumbent, silvery white, simple setae apically; such setae becoming more abundant on more apical terga, most notably terga V and VI, intermixed with slightly longer suberect setae; sterna with similar subappressed to suberect setae apically, progressively setae more broadly present on more apical sterna.

Queen. Total body length 5.95 mm, forewing length (apex of costal sclerite to wing tip) 2.50 mm. Head slightly wider than long, width 1.04 mm, length 1.00 mm; compound eye length 0.65 mm; upper interorbital distance 0.73 mm, lower interorbital distance 0.71 mm. Scape length 0.50 mm, as long as torulocellar distance, torulocellar distance 0.50 mm. Clypeus broader than long, approximately 2× as wide as long, length 0.24 mm, width 0.50 mm. Malar area prominent, length approximately 1.8× flagellar diameter. Mandible narrower than that of worker, with a single, small preapical tooth. Intertegular distance 0.94 mm. Forewing with veins more yellowish than in worker, membrane hyaline, slightly tinged yellow like pale parchment; hind wing with 5 distal hamuli. Metatibia 3.1× as long as wide, length 0.69 mm, maximum width 0.22 mm; outer surface uniformly convex. Propodeum with exceedingly short basal area, broadly rounding into sloping posterior surface. Metasoma physogastric (fig. 5).

Integument of clypeus and face smooth and shining with minute, scattered setigerous punctures (fig. 6A); gena largely smooth and glabrous; postgena smooth and glabrous except setigerous punctures medially bordering hypostomal fossa, and at border with occiput. Pronotum smooth with scattered minute, setigerous punctures; mesoscutum smooth with scattered minute setigerous punctures (fig. 6B); mesoscutellum as on mesoscutum except punctures more widely spaced and those in posterior half slightly larger, axilla sculptured as on mesoscutum, preaxilla and mesoscutellar crest impunctate; metanotum with abundant minute, setigerous punctures; mesepisternum smooth with minute, setigerous punctures, such punctures becoming more widely spaced posteriorly with virtually glabrous space ventral to hypoepimeral area; metepisternum smooth with minute, setigerous punctures confined to upper quarter near wing base; basal area and posterior surface of propodeum smooth and glabrous, lateral surface with minute setigerous punctures as on anterior half of mesepisternum. Metasomal tergum I largely smooth and glabrous except some setigerous punctures anterolaterally and posteriorly; tergum II smooth with scattered, setigerous, postgradular punctures; terga III–VI smooth with more abundant and uniform setigerous punctures; sterna smooth to faintly coriarious with setigerous punctures in apical halves of discs, except sternum VI with more abundant and uniform postgradular setigerous punctures.

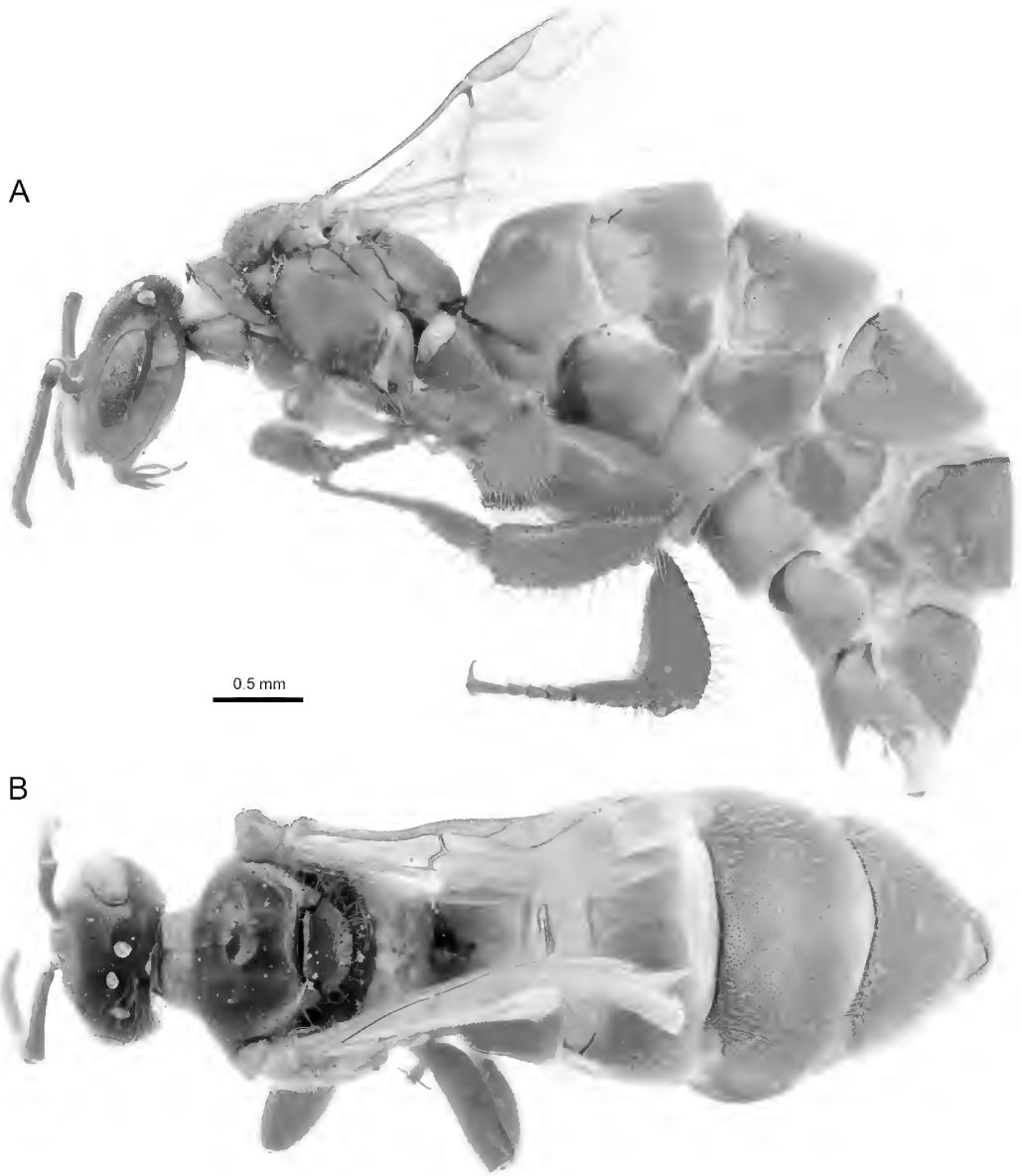


FIGURE 5. Queen of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Lateral habitus. **B.** Dorsal habitus.

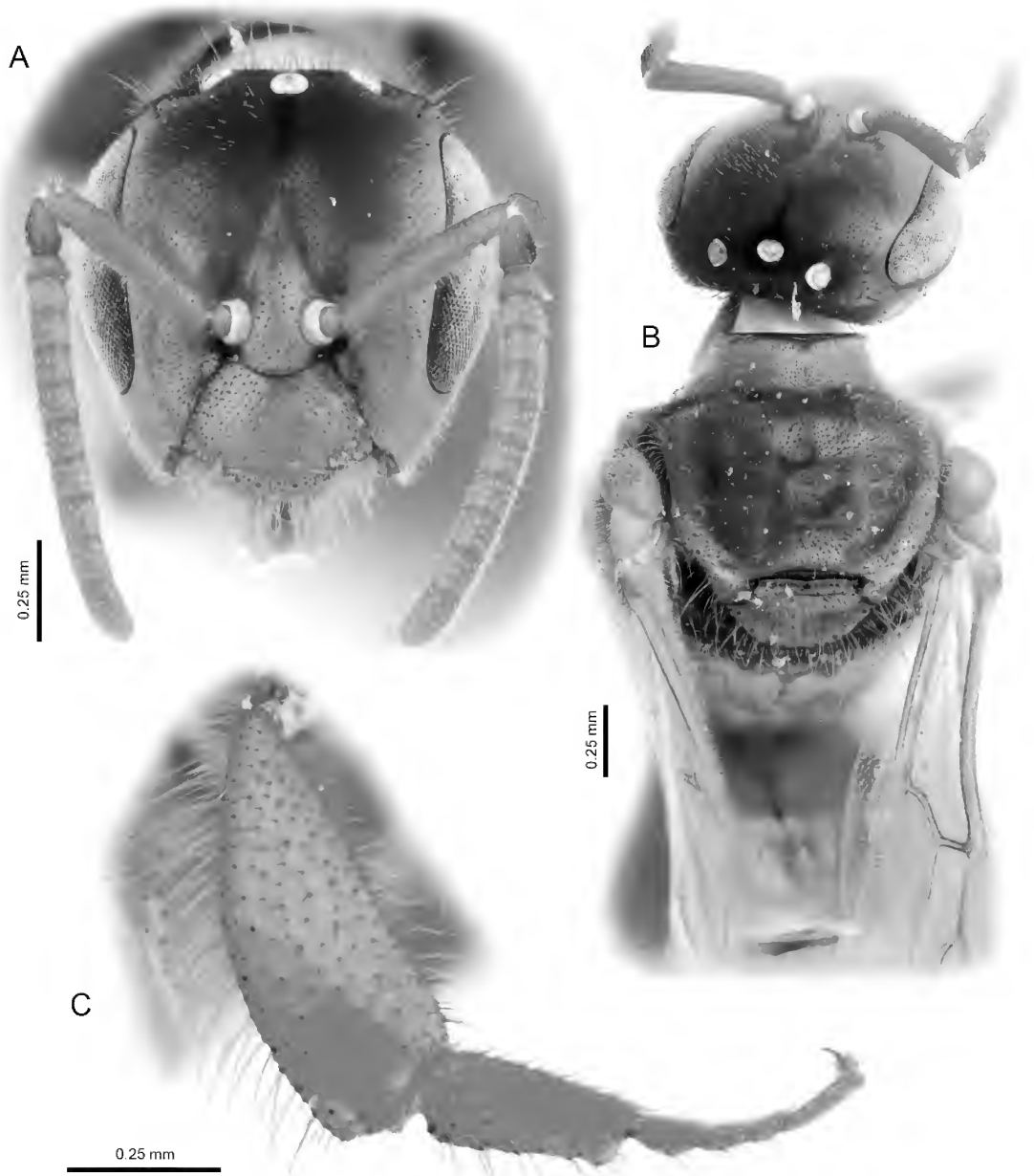


FIGURE 6. Queen of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Facial view. **B.** Dorsal detail of head and mesosoma. **C.** Outer surface of metatibia and metatarsus.

Integument generally yellowish orange to pale yellow (fig. 5), largely semitranslucent on mesosoma and portions of metasoma such that internal musculature can be observed in places; more brown on face above antennal toruli and between paraocular borders, apical half of pedicel, on vertex, uppermost gena, disc of mesoscutum, mesoscutellum, lower posterior mesepisternum, and ventral portion of metepisternum, with preaxilla, mesoscutellar crest, metanotum, and intercoxal region of metepisternum dark brown; wing veins pale yellow, membranes hyaline, clear.

Pubescence generally pale yellow to orange. Labrum with scattered elongate, erect, yellow setae; face with scattered minute, erect to suberect, yellow, simple setae; vertex posterior to ocelli with long, erect, simple setae; scape with minute, erect to suberect, simple setae, much shorter than diameter of scape; gena and postgena largely glabrous, except postgena with elongate, erect, simple, yellow setae bordering hypostomal fossa and long, erect, simple setae bordering occiput. Pronotum with numerous short, erect, fine, simple, white setae; mesoscutum with similar short setae as those on pronotum, intermixed with sparser elongate, erect, simple, white to yellowish setae; mesoscutellum with fine white setae slightly longer and sparser than those on mesoscutum, with elongate setae more numerous and somewhat longer, particularly along posterior border; metanotum with numerous exceptionally fine, short, white, simple setae; mesepisternum with short, erect, simple, yellowish setae, such setae becoming sparser posteriorly and slightly longer and paler ventrally, virtually glabrous posteriorly below hypoepimeral area; metepisternum virtually glabrous except with setae similar to mesepisternum in upper quarter near wing base; propodeum largely glabrous except laterally with scattered exceedingly fine, long, erect, simple, white setae, such setae more prominent around propodeal spiracle, with some longer, thicker, erect, simple, yellowish setae laterally bordering posterior surface. Setae of legs largely pale yellow to off-white; setae of tibiae and basitarsi particularly abundant; setae of metatibia long and rather uniformly distributed, those posteriorly greatly elongate; penicillum, rastellum, and parapenicillum absent (fig. 6C). Metasomal tergum I sparsely setose, with some fine, erect to suberect, simple, off-white setae laterally on upper anterior-facing surface; tergum II with abundant fine, erect to suberect, simple, off-white setae on postgradular disc, such setae slightly more numerous posteriorly than anteriorly and sparser basally and medially; terga III–V with uniformly dense fine, erect to suberect, simple, off-white setae forming distinctive setal mats; tergum VI with setae similar to preceding terga except slightly more spaced and gradually becoming thicker and greatly more elongate apically; sterna with sparse, long to elongate, erect, simple, yellowish to off-white setae in apical portions of discs; sternum VI with such setae more abundant somewhat longer and intermixed over entire disc with fine, short, erect, off-white setae.

Drone. Total body length 2.87–3.00 mm, forewing length (apex of costal sclerite to wing tip) 2.13–2.17 mm. Head wider than long, width 0.98–1.02 mm, length 0.83–0.90 mm; compound eye length 0.71–0.73 mm; upper interorbital distance 0.60–0.65 mm, lower interorbital distance 0.42–0.44 mm. Scape length 0.27–0.29 mm, much shorter than torulocellar distance, torulocellar distance 0.40–0.44 mm. Clypeus broader than long, approximately 1.8× as wide as long, length 0.21–0.24 mm, width 0.38–0.42 mm. Malar area linear, with mandibular base

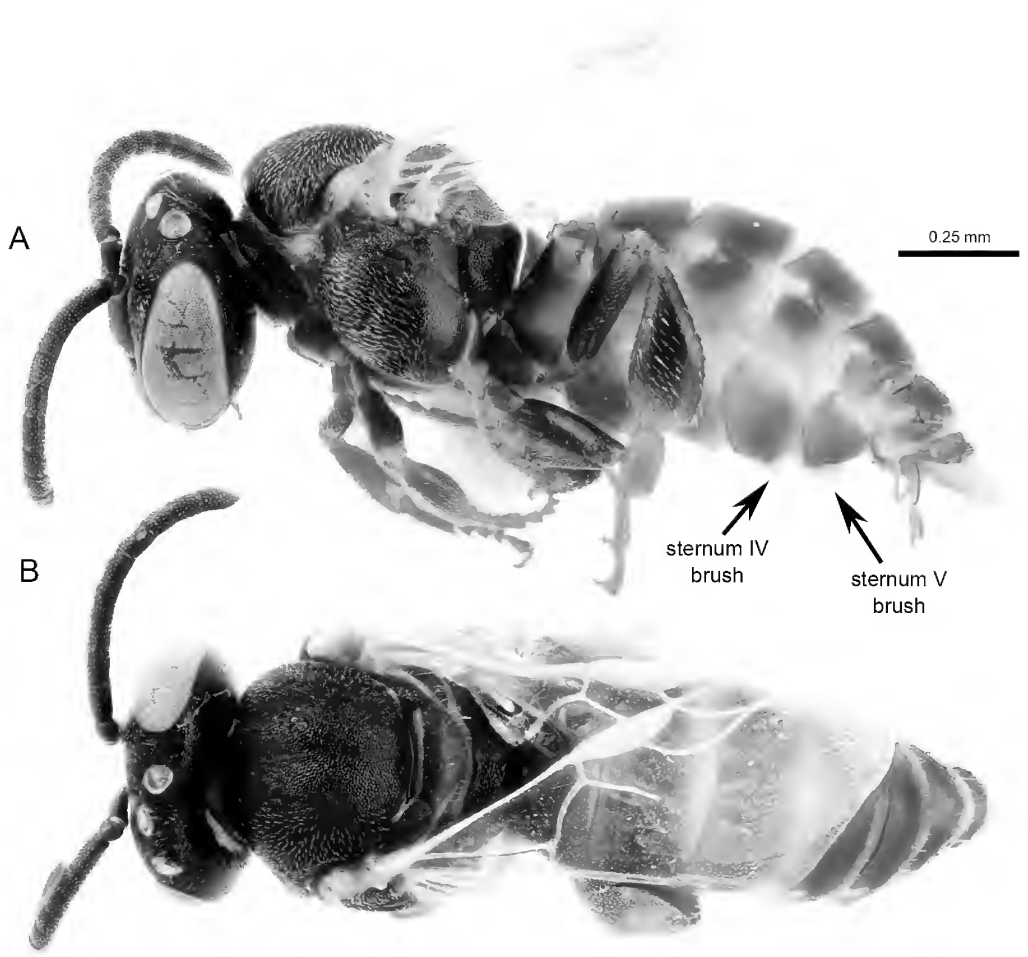


FIGURE 7. Drone of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Lateral habitus. **B.** Dorsal habitus.

appearing to abut lower compound eye margin (fig. 8A). Metatibia 2.6–2.7× as long as wide (fig. 8B), length 0.77–0.78 mm, maximum width 0.28–0.30 mm; outer surface uniformly convex. Propodeum as in worker. Forewing as in worker except basal angle more acute, 73°, with R on wing margin beyond pterostigma slightly longer than marginal cell width at pterostigmal apex; hind wing with 5 distal hamuli. Modified sterna IV and V, hidden sterna VI and VII, and genital capsule as depicted in figure 9.

Integumental sculpturing as described for worker (fig. 7).

Coloration as described for worker except as follows: pale yellow on labiomaxillary complex, mandibles, and labrum (fig. 8A) (clypeus dark brown); antennal scape yellowish on lower surface and brown on much of upper surface; pedicel pale brown to brown; flagellum brown

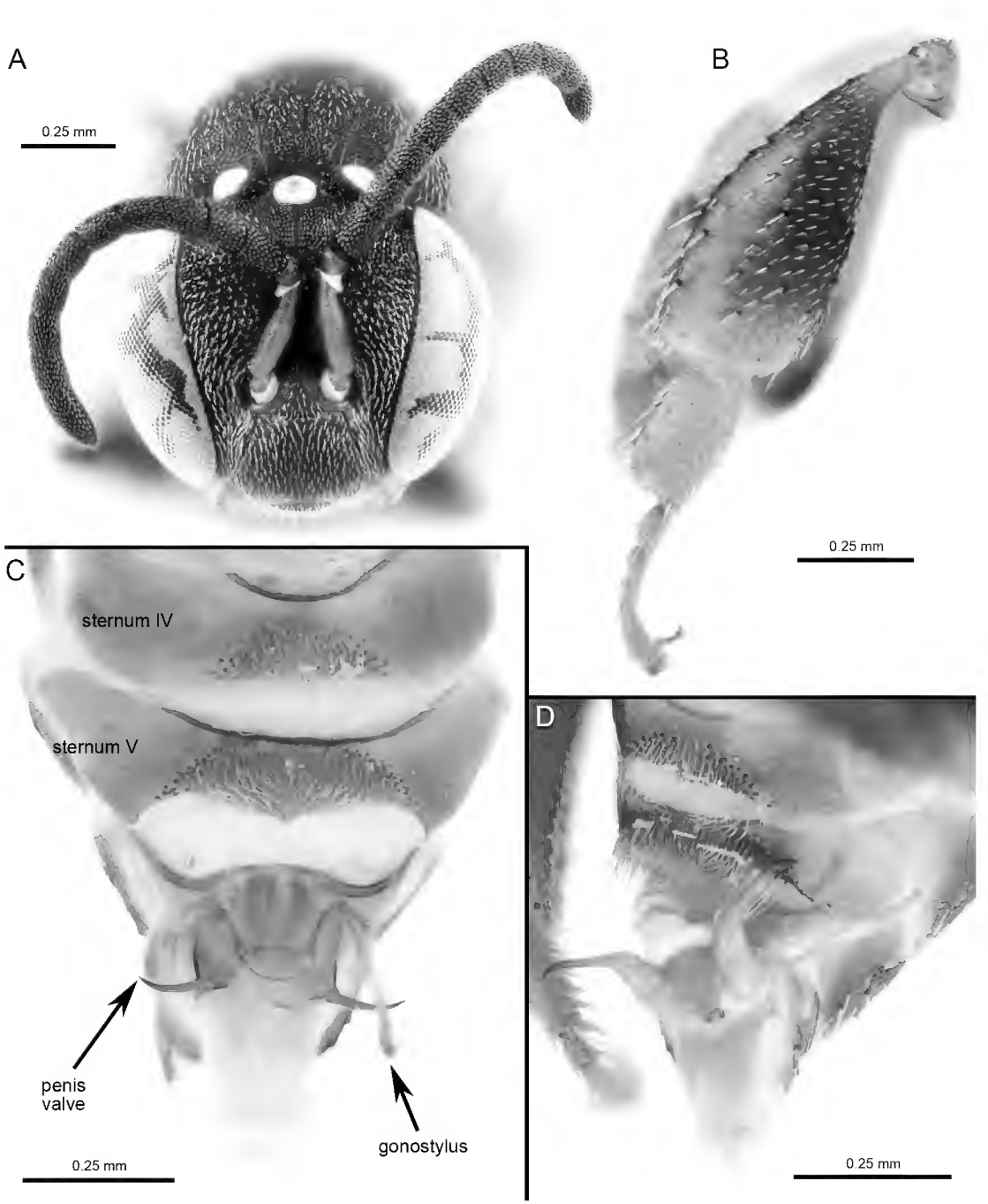


FIGURE 8. Drone of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Facial view. **B.** Outer surface of metatibia and metatarsus. **C.** Ventral view of metasomal apex. **D.** Ventral oblique aspect of metasomal apex, showing length and angulation of setae on sternal brushes.

to dark brown. Pronotal collar brown to dark brown, with pronotal lobe yellow to pale brown (fig. 7A), sometimes with posterior borders and posterior dorsal ridge long mesoscutum yellow to pale brown; propleuron pale brown to brown; axilla dark brown to brown, mesoscutellum frequently lighter than axillae, brown to pale brown; metanotum brown to yellowish brown; procoxa, protrochanter, and profemur brown, protibia brown to light brown on outer surface and lighter basally and apically, with inner surface largely light brown to yellowish brown, protarsus yellow; midleg largely brown to dark brown except mesotrochanter lighter, mesofemur with light brown to yellowish-brown apex, mesobasitarsus dark brown to brown on outer surface except lighter basally and apically, with inner surface largely light brown to yellowish brown, mesotarsus yellow; hind leg largely brown to dark brown, except lighter on metatrochanter, yellowish brown to light brown at apex of metafemur, basally and apically on metatibia, and yellowish on metatarsus.

Pubescence as described for worker except as follows: metatibia with minute to short, decumbent to subappressed simple, silvery white to off-white setae on outer surface, except for nearly glabrous strip posteriorly from about midlength to apex, posterior to glabrous strip setae long, particularly along posterior margin, apical margin with a line of minute, fine, simple, silvery- to off-white setae; worker specializations (e.g., penicillus, rastellum, parapenicillus) absent. Metasoma sparsely setose; sternum III with small lunular patch of long, fine, yellow to off-white setae medially at apical margin, setae characteristically kinked medioposteriorly at apexes; sternum IV with larger lunular patch of similar setae medially at apical margin (figs. 7A, 8C, D), lunular patch proximally well separated from gradulus, surface of lunular patch more flattened than remainder of sternum, apical margin bordering lunular patch roughly straight; sternum V with similar lunular patch of setae encompassing majority of disc and proximally meeting gradulus (figs. 7A, 8C, D), proximal margin of lunular patch area slightly ridged and flattened relative to remainder of sternum, with apical margin of sternum broadly concave except short, medioapical projection; setae of gonostylus as depicted in figures 8C, 9C.

Holotype: ♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, superior nest portion [taken from upper part of nest] (SEMC).

Paratypes (280♀♀, 1♀, 25♂♂): **Workers:** 101♀♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, superior nest portion [taken from upper part of nest] (91♀♀ SEMC, 2♀♀ AMNH, 2♀♀ BBSL, 2♀♀ LABUN, 1♀ ICNC, 2♀♀ PCYU, 1♀ IIRB); 123♀♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, inferior nest portion [taken from lower part of nest] (115♀♀ SEMC, 1♀ AMNH, 1♀ LABUN, 2♀♀ LIPI, 1♀ ICNC, 1♀ IIRB, 2♀♀ ZMHB); 8♀♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 18-xi-2016 [18 November 2016], M.S. Engel and V.H. Gonzalez, *Trigonisca* from nest entrance (SEMC); 21♀♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 18-xi-2016 [18 November 2016], M.S. Engel and V.H. Gonzalez (SEMC); 4♀♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 19-xi-2016 [19 November 2016], M.S. Engel

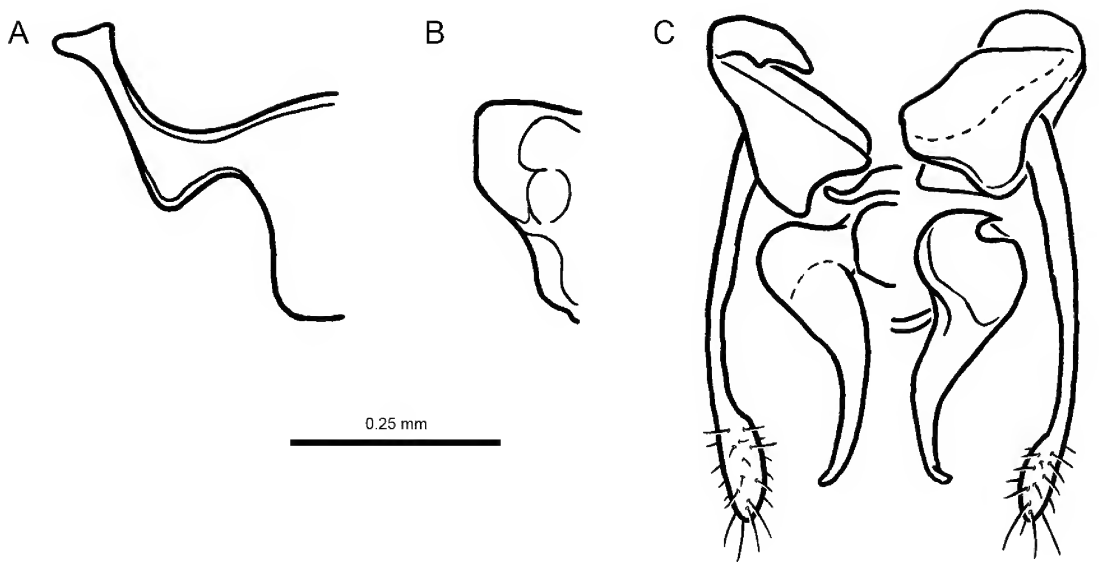


FIGURE 9. Male terminalia of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Sternum VI. **B.** Sternum VII. **C.** Genital capsule (left half is dorsal, right half is ventral).

and V.H. Gonzalez, ex: white pan trap (SEMC); 1♀, Colombia: La Guajira, Maicao, Yutaho, 11°24′47.69″N, 72°24′28.32″W, 19-xi-2016 [19 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, ex: yellow pan trap (SEMC); 1♀, Colombia: La Guajira, Maicao, Yutaho, 11°24′47.69″N, 72°24′28.32″W, 19-xi-2016 [19 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, ex: white pan trap (SEMC); 3♀♀, Colombia: La Guajira, Albania, Aulaulia, 11°20′15.28″N, 72°26′57.22″W, 19-xi-2016 [19 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda (SEMC); 1♀, Colombia: La Guajira, Albania, Aulaulia, 11°20′15.28″N, 72°26′57.22″W, 19-xi-2016 [19 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, ex: cactus nest (SEMC); 17♀♀, Colombia: La Guajira, Albania, Aulaulia, 11°20′15.28″N, 72°26′57.22″W, 19-xi-2016 [19 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, ex: double entrance nest (SEMC).

Queen: 1♀, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, superior nest portion [taken from upper part of nest] (SEMC).

Drones: 23♂♂, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, superior nest portion [taken from upper part of nest] (19♂♂ SEMC, 1♂ BBSL, 1♂ LABUN, 1♂ PCYU, 1♂ IIRB); 2♂♂, Colombia: La Guajira, Manaure, Pájaro, 11°31′43.91″N, 72°46′35.33″W, 20-xi-2016 [20 November 2016], M.S. Engel, V.H. Gonzalez, P. Sepúlveda, inferior nest portion [taken from lower part of nest] (1♂ SEMC, 1♂ AMNH).

ETYMOLOGY: The epithet of this species is the local name in the Wayuunaiki language given by the Wayúu indigenous people of La Guajira, Colombia. The name is treated as a noun in apposition.

COMMENTS: Among the large series of paratype workers and drones there are included several callow individuals, exhibiting those variations typical of early integumental coloration right after emergence.

IMMATURE STAGES

Egg

Figure 10

No well-preserved eggs of *T. mepecheu* were discovered. However, much of a single damaged egg was identified and examined with an SEM (fig. 10A). It is obviously small and slender, and its posterior end appears to be slightly wider than the anterior one. At approximate midbody, its diameter measures 0.317 mm; its estimated length will probably be around 1.1 mm. Its chorionic surface pattern consists of elevated geometric figures (hexagons, pentagons, etc.: fig. 10) with the patterning becoming elongate where approaching the micropyle (fig. 10B, E). The egg's posterior end was torn away so that it is uncertain whether it has any chorionic patterning.

MATERIAL STUDIED: One egg; same locality and date as holotype.

Mature Postdefecating Larva

Figures 11, 12

DIAGNOSIS: Like mature larvae of other Meliponini recently described, that of *T. mepecheu* exhibits (1) a mandible that tapers strongly to a narrow, slender apex, bearing sharp-pointed teeth and (2) most body segments each with a pair of dorsolateral tubercles. Furthermore, the first three body segments are robust and not attenuated, as they are in the Euglossini. As the smallest meliponine larva described so far, its size helps to distinguish it from most other tribal members. Its head in frontal view (fig. 12B) is extremely wide and flat and will probably be an identifying feature when mature larvae of other Meliponini are known.

DESCRIPTION: *Head:* Size moderate relative to body size (figs. 11, 12A); front of head in lateral profile relatively flat below narrow vertex, so that in oblique lateral view (fig. 12E) frons, clypeus, and labrum closely aligned; head capsule very broad (fig. 12D); vertex not bilobed in frontal view (fig. 12D). Condition of tentorium unknown; posterior tentorial pits normal in position; posterior thickening of head capsule narrow, scarcely bending forward medially as seen in dorsal view; internal coronal ridge absent; epistomal ridge on cleared head capsule evident from anterior mandibular articulation to anterior tentorial pit but fading out immediately mesad of anterior tentorial pits (fig. 12D: ATP); front of head capsule with transverse depression short distance above each antenna (fig. 12D, E, arrows); integument of head capsule mesad of each parietal band (fig. 12D) uneven presumably because of weak sclerotization. Parietal bands evident (fig. 12D, E). Antennal papilla (fig. 12D) circular at base, somewhat swollen but questionably conical in shape;

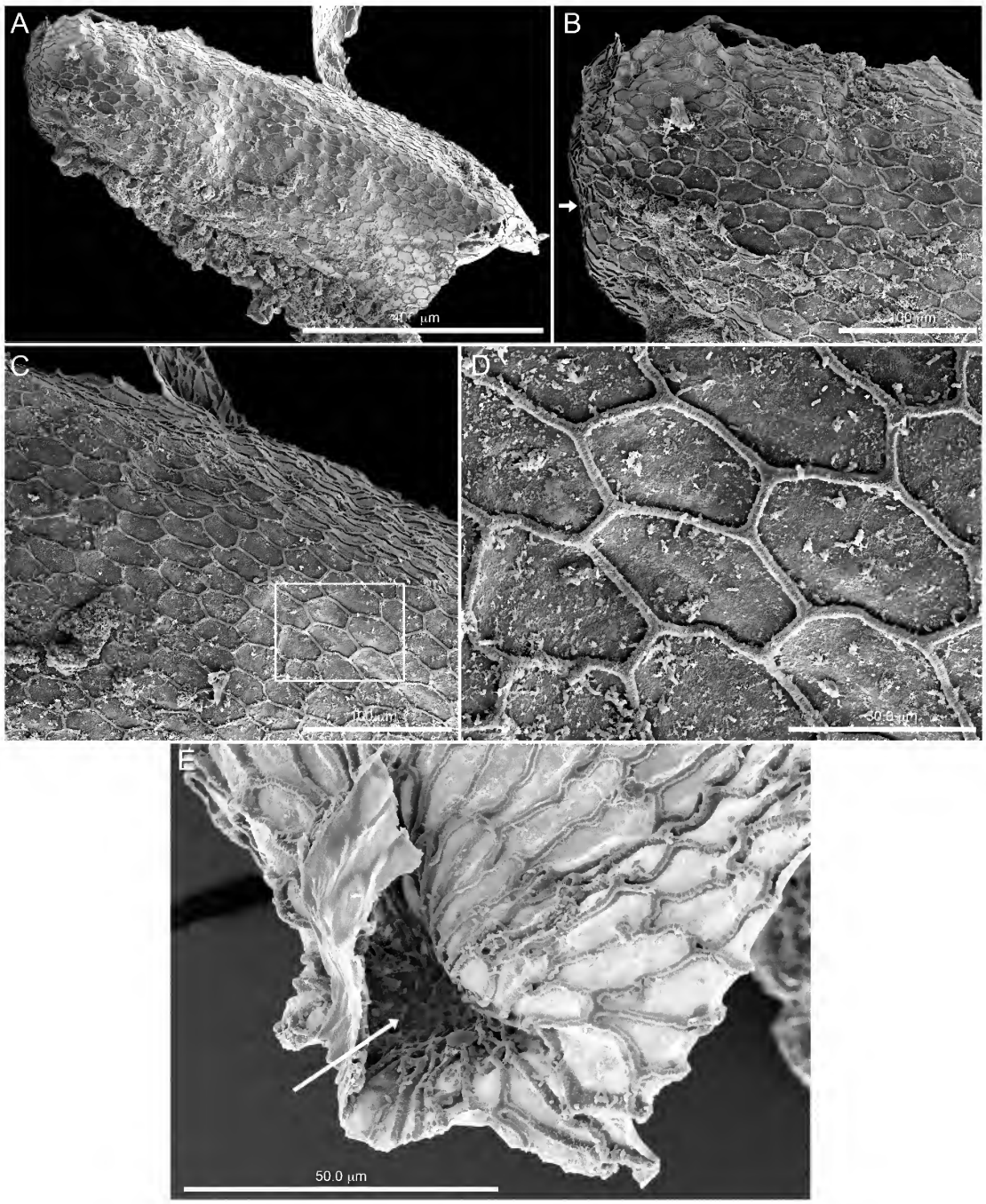


FIGURE 10. SEM micrograph of the damaged egg of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Egg full length with anterior end upper left. **B.** Anterior end showing hexagonal chorionic pattern becoming elongated toward micropyle (arrow). **C.** Close-up of hexagonal patterning at midbody. **D.** Close-up of rectangle in C. **E.** Micropyle (arrow) and adjoining chorion removed from egg.

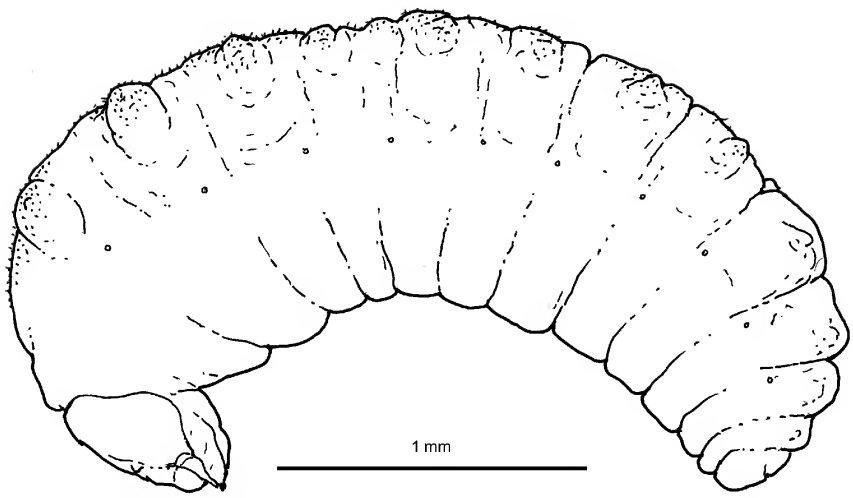


FIGURE 11. Diagram of entire mature larva of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, lateral view, head toward left, showing distribution of paired segmental dorsolateral body tubercles and small size of larva.

papilla bearing perhaps 3–4 inconspicuous sensilla; papilla surrounded by membranous ring with radius about one-half basal diameter papilla. Vertex curved in lateral view; frontoclypeal area not projecting beyond labrum (fig. 12E); apical surface of labrum bearing extensive patch of elongate, multipronged spicules (fig. 12D, F, G) medially.

Mandibular apex pigmented; mandible (fig. 12D, F) slender, elongate, narrowing evenly from broad base to pointed apex; apical concavity a narrow, elongate flattened surface considerably longer than distance from mandibular base at base of cusp; dorsal edge of apical concavity with numerous long slender sharp teeth as seen in exterior view (fig. 12G: lower right corner); ventral edge smoother than dorsal edge; apex (fig. 12F) sharply pointed; cusp not projecting but inner surface uneven.

Labiomaxillary region variably projecting relative to head capsule in lateral view; labium and maxilla extending more or less equally in lateral view (fig. 11). Maxillary apex not bent mesad; palpus apical in position, more than twice as long as basal diameter; galea evident at maxillary apex, bearing several sensilla; articulating arm of stipes questionably present; basal articulation of stipes to cardo clearly defined; dorsal and inner apical surface of maxilla spiculate. Labium divided into prementum and postmentum, bearing apically projecting broad lips of slitlike salivary opening that is slightly shorter than distance between bases of labial palpi (fig. 12D); length of labial palpus about twice basal diameter. Hypopharynx spiculate.

Body: Dorsal integument of body from posterior margin of head toward posterior end more or less densely covered with fine spicules (figs. 11, 12A–C) that extend just laterad of each paired dorsal body tubercles (identified below); density of spicules gradually diminishing toward rear of abdomen. Each thoracic segment (figs. 11, 12A, B) with pair of small but distinct elevated dorsolateral tubercles on caudal annulet; abdominal segments

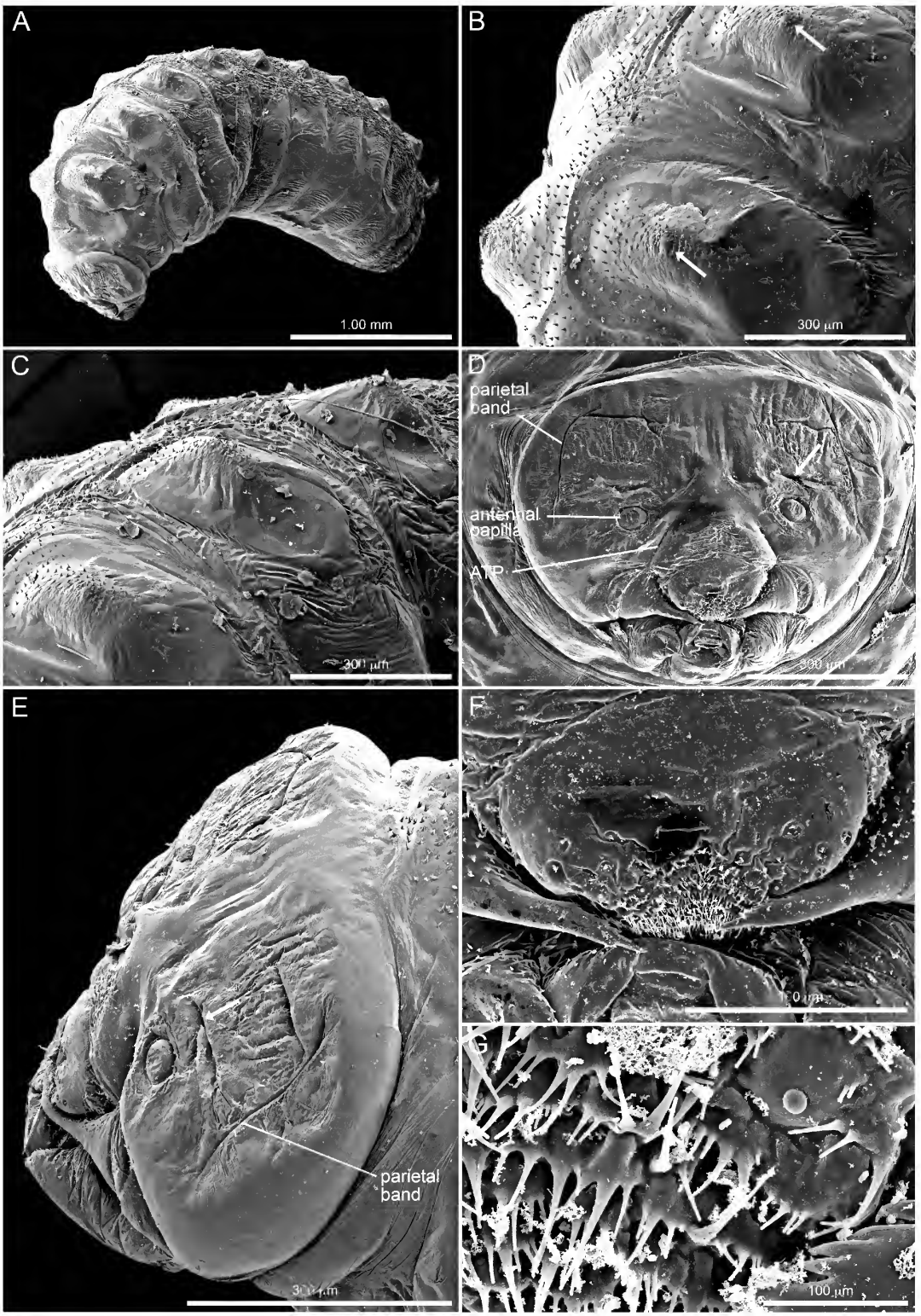
1–6 (figs. 11, 12A, C) also each with paired dorsolateral tubercles that become smaller and less pronounced toward posterior end of body. When larva cleared and stained with Chlorazol Black E, these tubercles positioned on paired, slightly elevated, transversely oblong stained surfaces of caudal annulets; abdominal segments 7, 8 with paired transverse oblong darkly stained areas lacking tubercles. Spiracles moderate in size, peritreme distinct; atrium shallow; atrial wall smooth or nearly so; primary tracheal opening a simple rim, smaller than atrial opening; subatrium moderately short consisting of about six annulations; flexure collapsed into single, long narrow tube.

Material Studied: 10+ postdefecating larvae; same locality and date as holotype.

Comments: The SEM micrographs of this very small larva advances our knowledge concerning its anatomy, which in turn illuminates our understanding of the morphology of larval Meliponini. The front of the head in figure 12D is extremely broad relative to its length and quite flat. Its extensive width contrasts with the relatively restricted subtending mouthpart structures (mandibles, maxillae, and labium). The paired, nearly circular, domed antennae are clearly visible toward the center of the face, and a pair of dorsally converging, slitlike anterior tentorial pits (fig. 12D: ATP) can be identified mesad of and slightly below the level of the antennae. The extensive wrinkled area above each antenna extending almost to the dorsal edge of the head capsule suggests that the integument there is thin and yielding. In contrast, the smooth surface of the head capsule laterad of the mandibular bases is firm, thickly sclerotized as is the integument surrounding both anterior tentorial pits and the coronal midline of the head capsule. Although there is no internal epistomal ridge mesad the anterior tentorial pits nor an internal coronal ridge as often found in larval bees (e.g., *Bombus impatiens* Cresson, Rozen et al., 2018: fig. 54), the firm thickened integumental structure of these areas of the head capsule are still present. The two large integumental wrinkled areas laterad of the central coronal thickening occupy areas that are usually smooth curved surfaces on larvae of other bees (e.g., *B. impatiens*, Rozen et al., 2018: figs. 54, 55).

Another interesting feature exhibited in figure 12D is a fibrous patch centrally positioned on the lower apex of the labrum. When viewed under greater magnification (fig. 12F) it is seen to consist of long slender prongs branching from centrally clustered spicules surrounded by a dispersed field of nipplelike sensilla. From a more lateral orientation (fig. 12G), there is a suggestion that, in action, the upper serrated mandibular edge might possibly comb the prongs and thereby force food material into the buccal cavity. Observations of larger, live, related species perhaps might be able to explore the feeding action of mandibles and surrounding mouthparts in greater detail. The structure of these labral spicules is better understood and illustrated in Rozen et al. (2019: figs. 12–14) where each is seen to consist of a basal projection that divides into a transverse group of fine, tapering prongs. When these basal projections are very dense, they appear in some places to form a transverse ridge, as in the case of *T. mepecheu* (fig. 12G).

Because multipronged labral spicules certainly occur in *Trigonisca*, *Plebeia* Schwarz, and *Melipona* Illiger, it would not be surprising if other meliponines were found to have them.


A
1.00 mm
B
300 µm
C
300 µm
D
parietal band
antennal papilla
ATP
300 µm
E
parietal band
300 µm
F
100 µm
G
100 µm

NEST HABITS, ARCHITECTURE, AND ETHNOGRAPHIC DATA

Nesting habits: This species nests inside preexisting cavities in a wide range of substrates that included both natural and human-made constructions (figs. 13, 14). We found nests between 0.8 and 2 m above the ground (mean = 1.22 ± 0.46, $N = 7$), inside tombs of cemeteries, house walls, and both living and dead tree trunks. Most nests were inside tree trunks of living divi-divi trees (fig. 13) (*Libidibia coriaria* (Jacq.) Schltdl.; Fabaceae: Caesalpinioideae: Caesalpinieae) that ranged in diameter from 8.0 to 20 cm (mean = 14.80 ± 5.17, $N = 5$). We found three nests inside a living *Stenocereus griseus* (Haw.) Buxb. (fig. 14A) ("Mexican organ pipe" cactus) (Cactaceae: Cactoideae: Pachycereeae), a columnar cactus (8–10 cm in diameter) widely used by the Wayúu people in La Guajira (Villalobos et al., 2007). We found three nests in the same tree trunk and one nest had two entrances (fig. 13B).

The nest entrance consisted of a hard, black wax tube that projected only slightly from the entrance (length 2.00–6.00 mm, mean = 4.25 ± 1.71, $N = 4$) (figs. 13, 14). The nest entrance was oval, with a length ranging from 5.00 to 8.00 mm (mean = 6.38 ± 0.92, $N = 8$) and width from 3.00 to 6.00 mm (mean = 4.13 ± 0.99, $N = 8$). Between 8 and 10 workers guarded the nest entrance (fig. 14B, C, E), which rapidly retreated when disturbed.

Internal architecture: The nest was inside a living tree trunk of about 13 cm in diameter. It lacked of an involucrum and its brood cells were in clusters (figs. 15, 16), not in combs, inside an irregular cavity about 70 cm long and 0.4 to 3.9 cm wide (mean = 2.18 ± 1.41, $N = 6$). A drop of dark, sticky resin was near the nest entrance (fig. 16A). Pollen and honey pots were translucent brownish, were in the same cluster, either alone near the nest entrance or at the bottom of the cavity and mixed with brood cells (fig. 16). Pollen pots ranged from 3.02 to 4.04 mm in length (mean = 3.42 ± 0.24, $N = 4$) and 1.68 to 2.90 mm in diameter (mean = 2.30 ± 0.51, $N = 4$). Honey pots ranged from 3.16 to 5.30 mm in length (mean = 4.14 ± 0.62, $N = 3$) and 2.51 to 2.90 mm in diameter (mean = 2.64 ± 0.22, $N = 3$). The nest had at least 603 adults (some escaped during collection) and 1008 brood cells.

Ethnographic notes: This species is one of the two stingless bees we encountered in the localities around Riohacha that we visited, which the Wayúu people locally recognized as *mepeche'u* or *mepeku*. The other species is *Melipona favosa* (Fabricius) or *mapa'a* (fig. 17) (also spelled as *mapa* according to Álvarez, 2017: 217), which literally means "honey." The Wayúu do not manage them, but they extract and consume the honey of the species whenever they find a nest. According to them, the honey is useful to treat the common cold and people can extract up to 3 L of honey from nests of *M. favosa*. Our youngest informant (6 years old) told

FIGURE 12. SEM micrographs of mature larva of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species. **A.** Entire larva, oblique frontal view. **B.** Close-up of pro- and mesothoracic segments showing paired segmental dorsolateral tubercles (arrows) and distribution of fine spicules. **C.** Close-up of meso- and metathoracic segments and of first abdominal segment showing dorsolateral tubercles along left side as well as distribution of fine spicules. **D.** Head, frontal view, demonstrating extreme width, and showing pronounced, dome-shaped antennae. **E.** Same, oblique lateral view. **F.** Close-up of labrum and mandibles, frontal view, showing cluster of multipronged spicules at lower edge of labrum as well as sharp-pointed mandibles. **G.** Close-up of left side of cluster of multipronged spicules along lower edge of labrum and sharply toothed upper edge of left mandible, possibly used as comb to push provisions through prongs toward esophagus.

FIGURE 13. Nest of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, in La Guajira, Colombia (photographs by M.S. Engel). **A.** Location of nest in the side of a divi-divi tree (*Libidibia coriaria* (Jacq.) Schltdl.) (Fabaceae: Caesalpinioideae) (arrow shows position of nest entrance). **B.** Detail of nest entrance.

us that his grandmother warns him not to drink the honey of *T. mepecheu* because of the risk of becoming blind. This is the first report of a species of *Trigonisca* producing injurious honey. We were unable to determine whether this knowledge stems from myth or cultural memory of an incident (or incidents) in the past whereby consumption of honey from *T. mepecheu* resulted in illness. Honey produced by generalist bees can change over and between seasons depending on what flowers are in bloom and from which of them the bees are harvesting nectar and pollen. The most infamous and historical example is the harvesting from rhododendrons by workers of *Apis mellifera* L. (e.g., the fifth-century BCE writer Xenophon [1998]; Radt, 2005; Gunduz et al., 2011), the result of which is a nocent honey (called in some regions, "mad honey") that, when consumed, leads to serious medical complications and even death (Gunduz et al., 2006, 2008; Jansen et al., 2012; Sohn et al., 2014). Similarly, reports of nocuous honey from stingless bees are not unheard of (Schwarz, 1948; Lévi-Strauss, 1966, 1971), with particularly numerous indigenous accounts of toxic honey in the nests of *Lestrimelitta limao* (Smith) (reviewed by Schwarz, 1948). The consistent toxicity of honey by a robber bee such as *L. limao* seems to suggest that, at least in the case of this species, the bees themselves add some noxious secretions or selectively gather nectar from poisonous floral sources (Schwarz, 1948). Future research should explore the chemical and pollen composition of honey sampled from various

FIGURE 14. Nests of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, in La Guajira, Colombia (photographs by M.S. Engel). **A.** Nest in the side of an organ pipe cactus (*Stenocereus griseus* (Haw.) Buxb.) (Cactaceae: Cactoideae) (arrow shows position of nest entrance). **B.** Detail of nest entrance, from nest depicted in A. **C.** A single-opening entrance of a nest in *Libidibia coriaria* (Jacq.) Schltdl. (Fabaceae: Caesalpinioideae). **D.** Tomb in Riohacha cemetery, with nests embedded in sides (arrow indicates position of nest entrance). **E.** Detail of nest entrance, from nest depicted in D.

FIGURE 15. Sampled nest of *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, from La Guajira, Colombia (photographs by M.S. Engel). **A.** Section of *Libidibia coriaria* (Jacq.) Schltdl. (Fabaceae: Caesalpinioideae), with side removed to expose nest within. **B.** Detail of brood cells in situ. **C.** Detail of brood cells in situ.

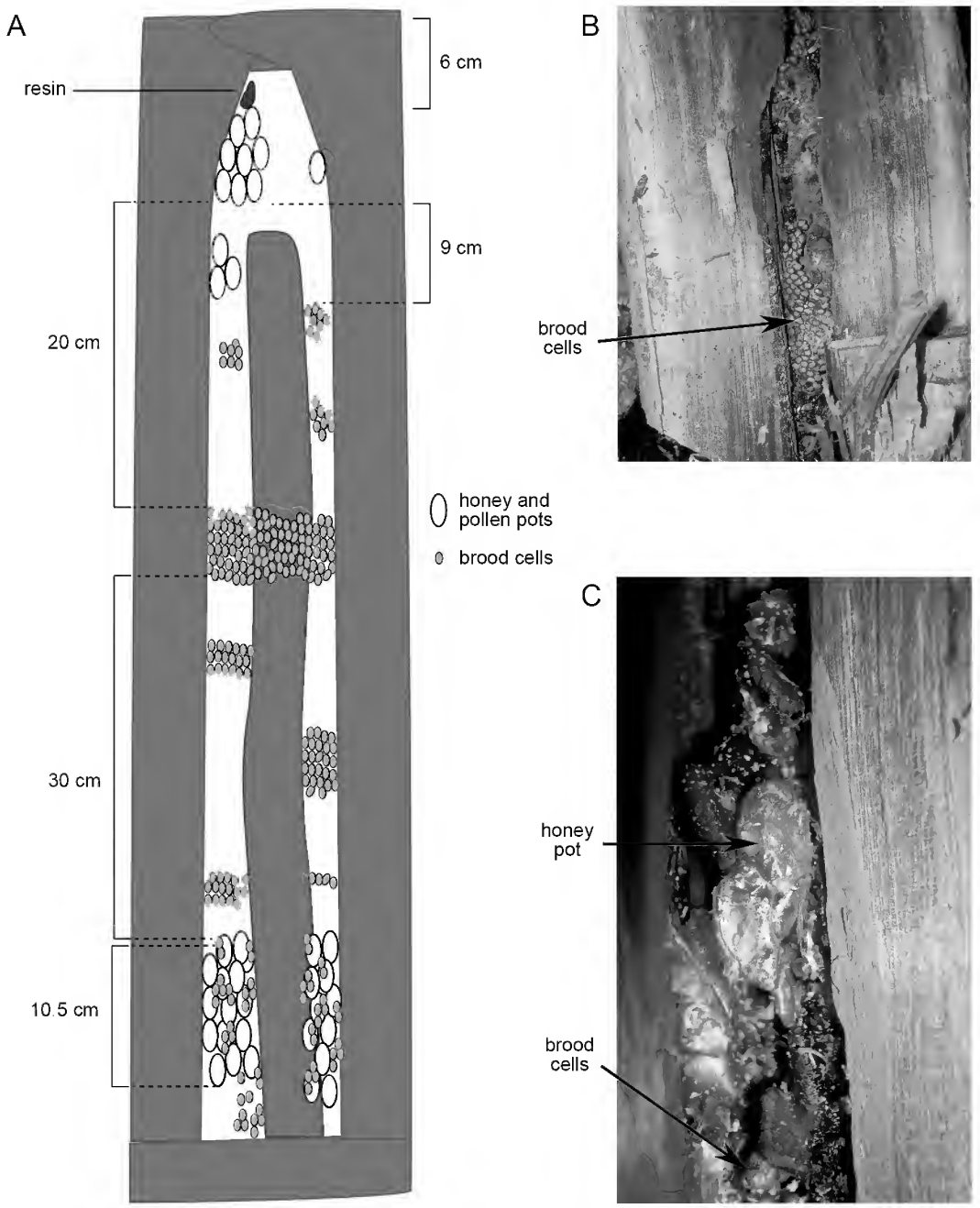


FIGURE 16. *Trigonisca* (*Trigonisca*) *mepecheu* Engel and Gonzalez, new species, from La Guajira, Colombia. **A.** Diagrammatic outline of sagittal section of nest and contents (note that nest entrance was removed and would be facing outward toward the viewer), **B.** Photograph of medial section of brood cells. **C.** Photograph of honey pots and brood cells.

FIGURE 17. Nest of *Melipona favosa* (Fabricius) in the base of a large *Libidibia coriaria* (Jacq.) Schltdl. (Fabaceae: Caesalpinioideae), in La Guajira, Colombia (photographs by M.S. Engel). **A.** Worker at entrance made of mud in a radiating pattern. **B.** Detail of guard at nest entrance. **C.** Worker departing nest entrance.

nests of *T. mepecheu* to determine whether the honey is toxic and, if so, whether this is intermittently the case and from what floral source the poisons originate.

While we found more than a dozen nests of *T. mepecheu*, we found only three nests of *M. favosa*. These nests were at the base of large divi-divi trees (fig. 17) (30–40 cm in diameter) or in branches of about 26 cm in diameter at 2.2 m above ground. *Melipona favosa* builds its nest entrance with mud and typically consists of a single opening (~6 mm in diameter) to which a series of distinctive striations converged (fig. 17A). The Wayúu also use the propolis of *M. favosa*, which they boil in water and then drink the mixture in order to treat seizures or tremors.

The Wayúu also recognized the exotic honey bee, *A. mellifera*, which is named either *mapa'a apricana* or *ko'oiyosu*. In some literature, honey bees are sometimes referred to as *ko'oi* only. However, we confirmed that people refer with this name to a honey wasp (Vespidae: *Brachygastra* sp.), which the Wayúu from the Sijuana caste in the Upper Guajira considered their ancestor (Freyle et al., 2003). For the Wayúu, other bees such as carpenter bees (Apidae: *Xylocopa* spp.), are not included in the same category with stingless bees because they do not make honey. This folk taxonomy resembles that of the Mixtec of Mexico (Gonzalez et al., 2018).

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